

A DESCRIPTION OF THE SKELETON OF A BAURIID  
THEROCEPHALIAN FROM THE EARLY TRIASSIC OF SOUTH AFRICA

By

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(With 10 figures)

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ABSTRACT

The postcranial skeleton of a baurioid therocephalian (NMQR 3189) from the *Cynognathus* Assemblage Zone of South Africa is described and compared to that of other therocephalians. The specimen constitutes the best-preserved skeleton of one of the latest therocephalians known. In the structure of the vertebral column and scapula, NMQR 3189 is very similar to the earliest therocephalians but it differs in the more gracile humerus, the absence of very small phalanges in the manus, and the large obturator foramen.

CONTENTS

	PAGE
Introduction .....	379
Description .....	380
Lower jaw .....	380
Axial skeleton .....	383
Pectoral girdle and forelimb .....	384
Pelvic girdle and hind limb .....	387
Conclusion .....	391
Acknowledgements .....	392
References .....	392
Abbreviations .....	393

INTRODUCTION

The postcranial skeleton of the therocephalian mammal-like reptiles has been described by various authors (Watson 1931; Broom 1937; Boonstra 1938, 1964; Schaeffer 1941; Attridge 1956; Cys 1967; Kemp 1978, 1986) but is still poorly known because complete and well-preserved skeletons are rare. A recently discovered specimen of a reasonably complete, associated but disarticulated skeleton will help to fill this gap and contribute to our understanding of the group.

In South Africa, the therocephalians have a relatively long stratigraphic history. Known from the lowest of the Late Permian Beaufort Group biozones, the *Eodicynodon-Tapinoctonus* Assemblage Zone (Rubidge 1990), the range of therocephalians extends into the *Cynognathus* Assemblage Zone (Rubidge in press).

Therocephalian postcranial material is currently known from several of the Beaufort assemblage zones. *Cynariognathus* Cys, 1967, is an example of an early therocephalian. It is from a locality in the *Tapinocephalus* zone (Kitching 1977), which may be equivalent to either the *Tapinocephalus* or *Pristerognathus*

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Assemblage Zone (Rubidge in press). Van den Heever (1987) considered the genus *Cynariognathus* to be invalid. However, he did not study the specimen described by Cys and therefore did not synonymize it with any other genus. For the purposes of this paper, the specimen will continue to be referred to as *Cynariognathus*.

Boonstra (1964) described postcranial elements of several genera from localities that probably include *Tapinocephalus* Assemblage Zone and *Pristerocephalus* Assemblage Zone rocks. *Mirotenthes* Attridge, 1956, is probably from the *Cistecephalus* Assemblage Zone, also Late Permian. *Ericiolacerta* Watson, 1931, and the regisaurid described by Kemp (1986) are both from the earliest Triassic *Lystrosaurus* Assemblage Zone.

The present specimen is from the *Cynognathus* Assemblage Zone. The only therocephalian of this age to be described in any detail is *Bauria cynops* (Broom 1937; Boonstra 1938; Schaeffer 1941) but, apart from the hind foot, no postcranial skeleton was described. The anterior skeleton of *Aelurognathus browni* (also from the *Cynognathus* Assemblage Zone) was described briefly by Broom (1906). The present specimen, therefore, makes an important contribution to our knowledge of the morphology of the late therocephalians.

This paper describes the postcranial skeleton of the newly discovered form and compares it with the skeleton of earlier therocephalians.

## DESCRIPTION

The specimen (National Museum, Bloemfontein, NMQR 3189) consists of a small block of mostly disarticulated skeletal elements in a soft grey-green matrix (Figs 1, 2). Although most postcranial elements are present, the only cranial material comprises the left ramus of the dentary and several isolated teeth.

The specimen comes from *Cynognathus* Assemblage Zone deposits on the farm Eerstegeluk 131 near Bethlehem, Free State Province, South Africa.

The most recent classification of the Therocephalia is that of Hopson & Barghusen (1986). Within their superfamily Baurioidea, the family Bauriidae is defined by several characters, only one of which can be partially verified in the present specimen: postcanine teeth greatly expanded transversely with crown-to-crown occlusion. Within the Therocephalia, this is a character unique to the Bauriidae and, in view of this, it is considered reasonable to identify the NMQR 3189 specimen as a member of that family. In fact, as shown below, the teeth are very similar to those of *Bauria* itself. The present specimen is provisionally identified as *Bauria cynops*, the only therocephalian known from the *Cynognathus* Assemblage Zone.

### LOWER JAW

Only the left ramus of the dentary is preserved and of this the anterior tip and its dentition are missing (Fig. 3). One complete tooth and the base of another are present at the preserved anterior end of the jaw. These are simple, pointed teeth followed by a short diastema. Next are four cheek teeth set in a deep trough in the dorsal surface of the jaw. The first three teeth increase in size posteriorly. The fourth tooth is damaged but appears to be smaller than the third. There appear to be no sockets for further teeth.

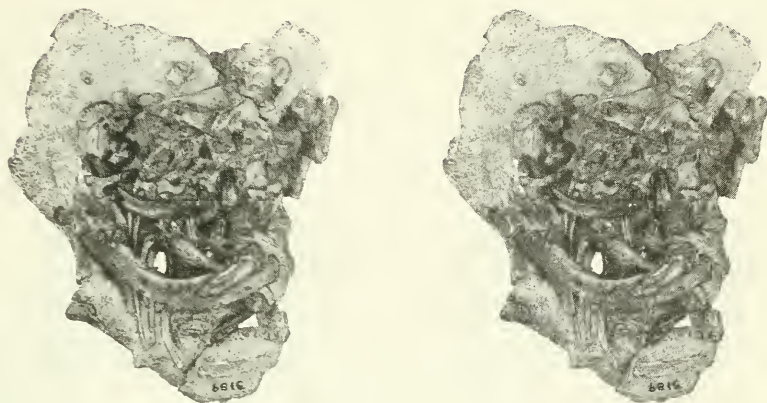


Fig. 1. The partly prepared block of matrix containing NMQR 3189 showing the lateral view of the dentary. Scale bar for photograph = 50 mm.

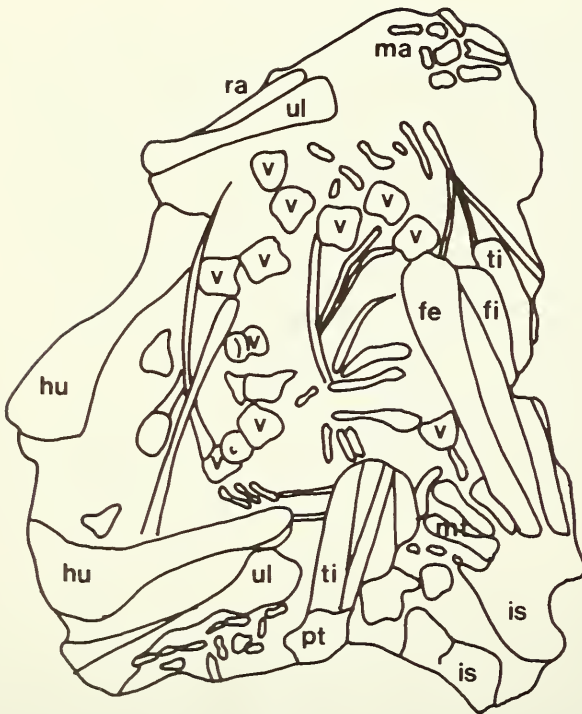
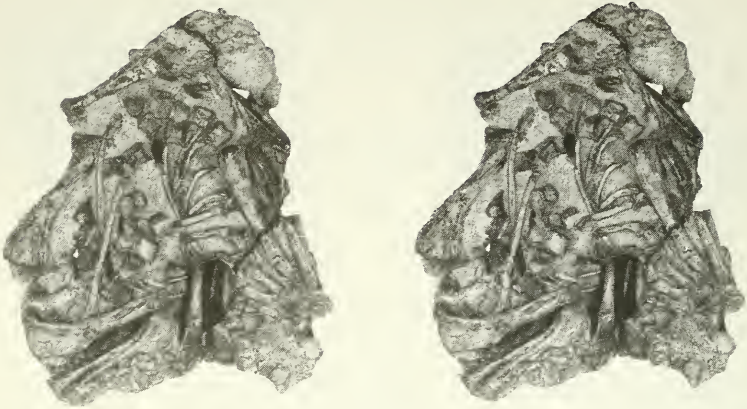


Fig. 2. The partly prepared block of matrix containing NMQR 3189 showing the long bones. Scale bar for photograph = 50 mm.



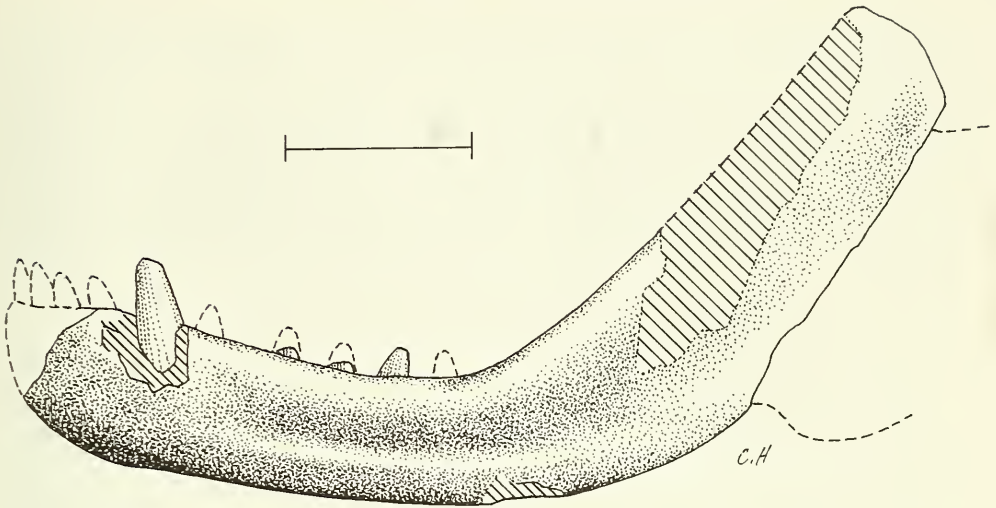


Fig. 3. The dentary of NMQR 3189 in lateral view. Missing bone is indicated by broken lines. Hatching indicates a covering of matrix or overlying bone. Scale bar = 10 mm.

The posterior teeth are expanded mediolaterally. Those with crowns preserved show one large lateral cusp and a ring of smaller cusps on the medial edge (Fig. 4), as described by Gow (1978) and Kemp (1982) for *Bauria*.

The lateral surface of the dentary is without feature apart from an elongated shallow depression that runs from just behind the symphysis to the base of the well-developed coronoid process.

What remains of the symphysis has a smooth, shallowly concave (mediolaterally) dorsal surface.

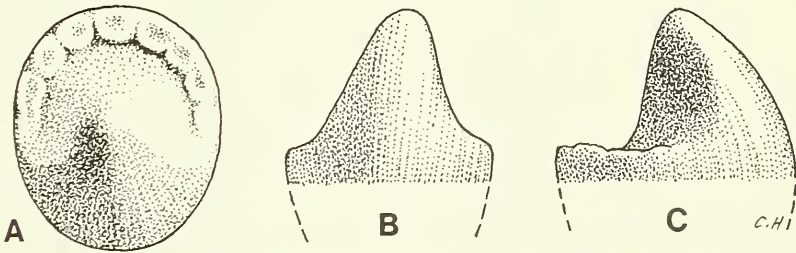


Fig. 4. The tooth crown (third most posterior tooth) of NMQR 3189. A. Dorsal view. B. Lateral view. C. Medial view.

#### AXIAL SKELETON

Approximately 20 vertebrae are present in the block. None is closely articulated to its neighbours, and neural arches and centra are frequently disassociated. Neural spines are low. The vertebrae are very similar to those described by Kemp (1986) in a regisaurid baurioid.

Approximately 15 ribs are preserved, the majority of which appear to be complete. The seven vertebrae that lie anterior to the sacrum (or thereabouts) are approximately in line and their ribs are almost in articulation. The transition from long, slender ribs to shorter, broader more horizontal ones can be seen clearly within this sequence. Attridge (1956) and Kemp (1986) also noted this transition in the specimens they described and considered that it might indicate the development of a transverse diaphragm. Kemp also thought it might be correlated with mammal-like features of the hind limb and its musculature. The transition can be seen clearly even in the early Karoo form, *Cynariognathus* (Cys 1967).

#### PECTORAL GIRDLE AND FORELIMB

Scapulae, clavicles, humeri, radii, ulnae and part of a manus are preserved.

The scapula (Fig. 5) is a delicate bone. The blade is narrow, flaring out somewhat dorsally. A marked depression runs down the lateral surface (Fig. 5—dep). Dorsally this begins near the anterior edge, but approaches the posterior edge more ventrally. The depression is bounded on its posterior side by a distinct ridge (Fig. 5—ri) that divides the scapular blade into two areas: a flat posterodorsal surface (Fig. 5—fs) and the anteroventral depression just described. The glenoid articulation is suboval. As in all known therocephalians, an acromion process is absent. A small scar for the triceps origin is present dorsal to the glenoid on the posterior edge of the bone.

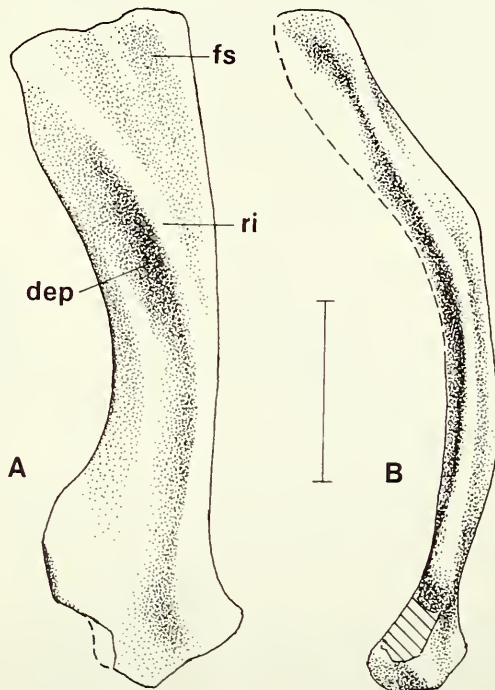


Fig. 5. The left scapula of NMQR 3189. A. Lateral view. B. Anterior view. Hatching indicates matrix and the broken line shows a restored outline. Scale bar = 10 mm.

The scapula of NMQR 3189 closely resembles that of *Eriaciolacerta* described by Watson (1931) and, although similar in general appearance to the regisaurid described by Kemp (1986), that specimen seems to lack the prominent ridge running across the scapular blade. The scapula of *Mirotenthes* described by Attridge (1956) is much narrower than that of NMQR 3189, but also shows the scapular ridge. The earliest of the described Karoo thercephalians, *Cynariognathus* (Cys 1967), is a much larger animal than those discussed so far and its scapula is correspondingly broader and more robust. As with the other forms, however, there is a pronounced depression on the lateral scapular surface, bounded by a ridge on the posterior edge.

The flat posterodorsal area of the scapular blade probably was the origin of the scapular deltoid, whereas the more ventral depression may have been the origin of the scapulo-humeralis anterior. The slenderness of the scapular blade limits the area available for muscle attachment and neither muscle could have been particularly well developed. However, the size of the anteroventral depression, extending as it does along most of the anterior surface of the scapular blade, provides ample room ventrally for a supracoracoideus attachment, and it is possible therefore that this muscle has extended its primitive origin on the coracoid to include part of the scapular blade. In this respect, NMQR 3189 would be more similar to the cynodont condition than the earlier regisaurid described by Kemp (1986).

The clavicle is a rod-shaped bone that fans out into a large rectangular plate proximally and into a smaller oval plate distally. Both proximal and distal ends are covered with numerous fine striations. The shaft of the clavicle is triangular in cross-section. The length of the clavicle is slightly less than that of the scapula. In overall shape, the clavicle is very similar to that of the baurioid described by Kemp (1986) but is longer and more delicate. The clavicle of *Eriaciolacerta* was described by Watson (1931) as being a powerful rod of bone; its proximal end is expanded as in Kemp's baurioid and NMQR 3189, but it appears to be somewhat shorter than in either of those two forms. The clavicle of *Cynariognathus* is a simple, somewhat robust, paddle-shaped element according to Cys (1967).

No other part of the ventral shoulder girdle is preserved.

The humerus (Fig. 6) is a slender bone with a distinct shaft. The proximal and distal ends are at a slight angle to one another. The ends are not well formed and distinct distal articular surfaces cannot be seen. The head of the bone (Fig. 6—hd) faces proximally as though the humerus took up a sprawling position at the glenoid. The entepicondylar foramen (Fig. 6—ent.f) is large and elongated. An ectepicondylar foramen is present. The delto-pectoral crest (Fig. 6—dpc) is not particularly well developed. The dorsal surface of the distal end bears a large fossa, presumably for part of the triceps insertion.

The humerus differs very little from that described by Kemp for his *Lystrosaurus-Procophon* Assemblage Zone specimen. Kemp considered that this humerus was held in a sprawling position. *Cynariognathus* (Cys 1967), from the *Tapinocephalus* Assemblage Zone, is a much larger animal and its humerus (approximately 180 mm in length) is more robust with well-marked articular surfaces, but otherwise similar. The humeri of *Mirotenthes* Attridge, 1956, and *Eriaciolacerta* Watson, 1931, are both very slender and have ends that



do not seem to be expanded. Both authors considered that the humerus in these forms was not held in a horizontal position but was more mammal-like as in cynodonts.

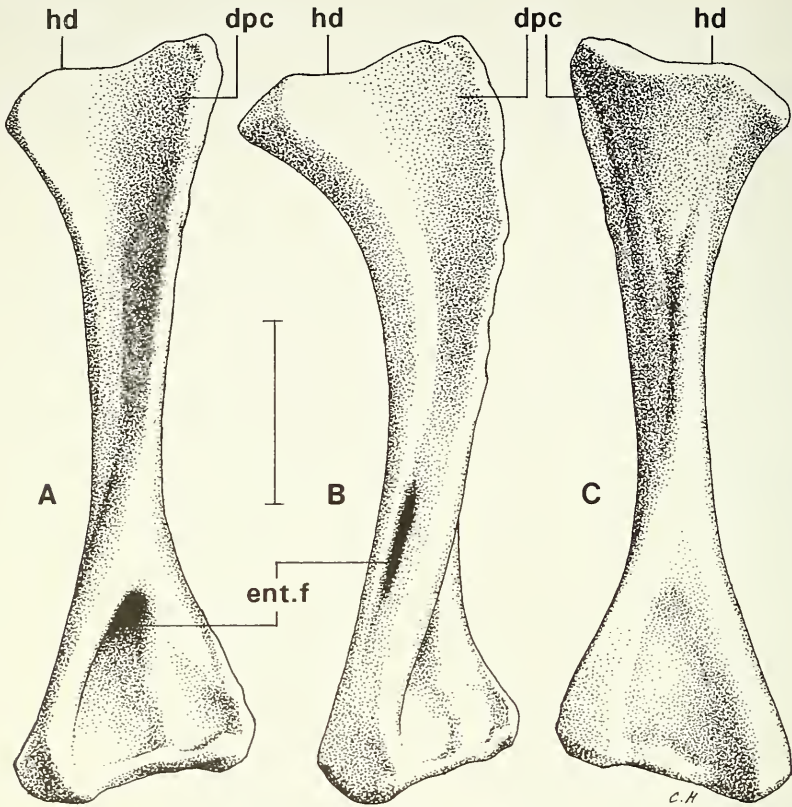


Fig. 6. The left humerus of NMQR 3189. A. Ventral view. B. Posterior view. C. Dorsal view. Scale bar = 10 mm.

The right radius and ulna are preserved *in situ* relative to one another and with a collection of disarticulated phalanges lying over the ulna. The left elements have been separated completely, but these are not as well preserved and appear to have been crushed.

Both radius and ulna are slender, rather delicate bones (Fig. 7). The ulna has a slight sigmoid curvature. It is markedly flattened anteroposteriorly. The proximal end of the ulna is expanded mediolaterally and proximally to form a weak olecranon process. There is a shallow trough on most of the posterior surface of the proximal end of the ulna. This trough is bounded laterally by a low rounded ridge. The distal end of the ulna is not expanded.

The radius has a more circular cross-section proximally than that of the ulna. Both ends of the radius are expanded and the proximal and distal surfaces are both elongated ovals. The proximal surface is markedly concave, that of the distal end shallowly concave.



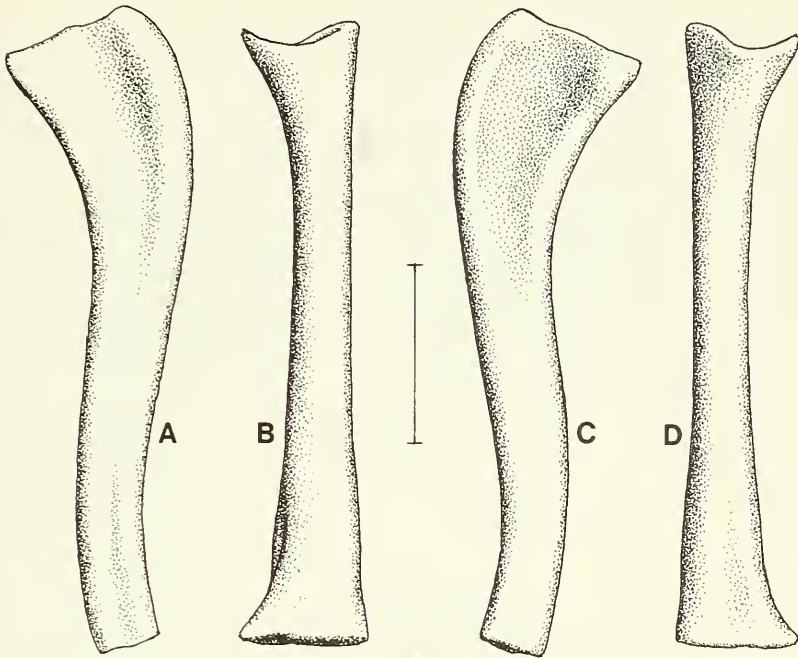


Fig. 7. The left radius and ulna of NMQR 3189. A. Ulna in anterior view. B. Radius in anterior view. C. Ulna in posterior view. D. Radius in posterior view. Scale bar = 10 mm.

Apart from the presence of the weakly developed olecranon process, very little distinguishes the radius and ulna of NMQR 3189 from those of the other described therocephalians.

Disarticulated phalanges are preserved close to the right radius and ulna, and partially articulated digits *in situ* by the left forearm. Little detail of the individual bones can be made out. The phalanges are delicate bones, approximately twice as long as wide, and the unguals are bluntly pointed claws. Very small phalanges, as illustrated by Cys (1967) for *Cynariognathus*, are not present.

#### PELVIC GIRDLE AND HIND LIMB

The ilia, ischia, femora, tibiae and fibulae are preserved, although no element is present in its entirety. Some elements of a partially disarticulated foot are also present. The pelvic girdle has been dorso-ventrally compressed so that the ilia meet the pubo-ischiadic plates at too small an angle. This distortion has been corrected in Figure 8C as shown in Figure 8B.

The greater part of the iliac blade is present, although the anterior end is missing from both right and left ilia, so that the extent of the anterior process is unknown (Figs 8, 9). The blade is a robust plate of bone bearing a large rectangular posterior process. Shallow concavities are present on the dorso-posterior part of the iliac blade, and also on what is present of the anterior part.

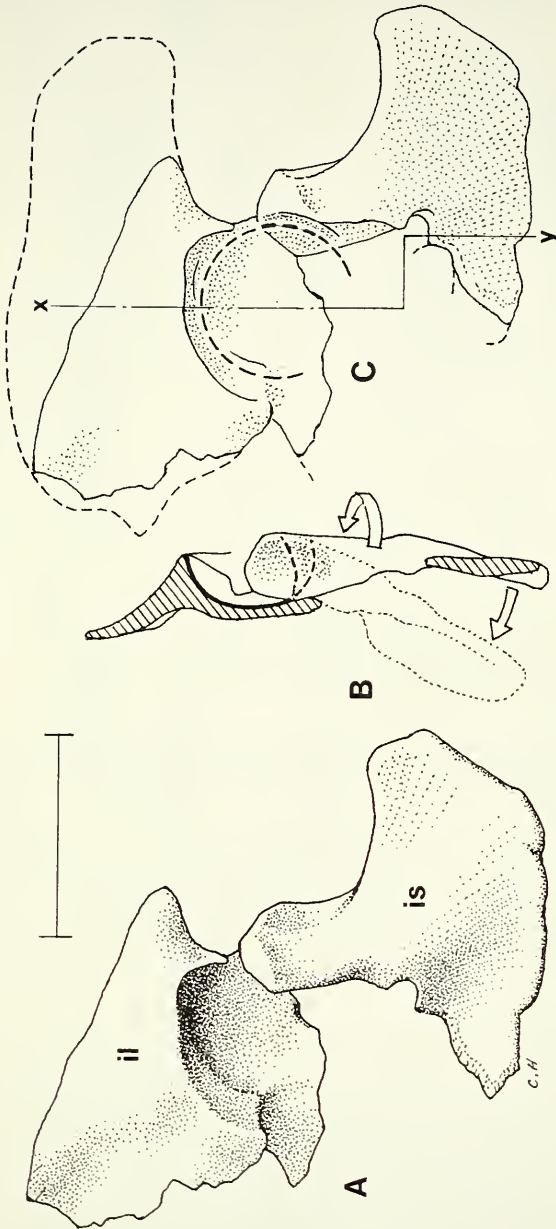


Fig. 8. The pelvis of NMQR 3189. A. Left ilium and ischium in lateral view. B. Diagram showing direction of rotation of the ischium from its preserved position to that reconstructed in (C). C. Reconstruction of the ilium and ischium in their presumed natural positions. Hatching indicates section through the bones. Line x-y shows planes of cross-sections in (B). Broken lines indicate restored outlines. Scale bar = 10 mm.

The ventral edge of the iliac blade forms the dorsal rim of the acetabulum with a distinct downwardly projecting lip. Sacral rib facets cannot be seen on the medial surface.

The ilium closely resembles that of *Regisaurus* (Kemp 1978) from the *Lystrosaurus* Assemblage Zone. The ilium of the baurioid from the same zone described by Kemp (1986) has a much smaller posterior process, but it is from a much smaller individual, which Kemp considered to be a juvenile. The ilium of the immature *Eriolacerta* described by Watson (1931) is extremely similar both in form and size to Kemp's specimen and Watson made the point that the shape of the pelvic bones might be different in an adult specimen. It is possible that the smaller posterior iliac process is a juvenile feature.

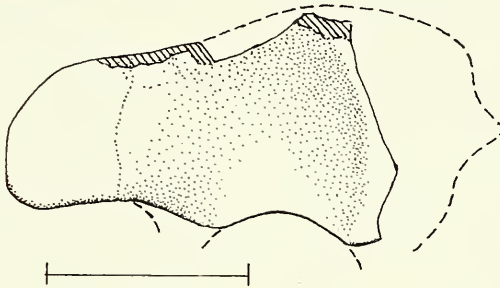


Fig. 9. The right ilium of NMQR 3189.  
Hatching indicates a covering of matrix.  
Broken lines indicate restored outline.  
Scale bar = 10 mm.

The posterior parts of both ischia are preserved (Fig. 8). The main body of the bone is a fairly thin oval plate that is constricted dorsally to form the ischial contribution to the acetabulum. The posterior edge is broad where it leads posteroventrally from the acetabulum, becoming thinner more posteroventrally.

A bone, which is probably the right pubis, was present near to the ischia. It is a rectangular plate of bone, one corner of which is produced dorsally to form the pubic contribution to the acetabulum. This is damaged in the present specimen but appears to have been small. From the acetabular portion, the plate is cut away to form the anterior edge of the large obturator fenestra. This edge is very thin, as is the anteroventral edge. The anterodorsal edge leading down from the acetabulum is thickened. The lateral surface of the plate is convex anteroposteriorly. Medially it bears a shallow fossa just ventral to the thickened anterior edge of the bone.

As in *Eriolacerta* and the baurioid described by Kemp (1986), the pubo-ischiadic plate of NMQR 3189 is larger than the ilium, with well-developed anterior and posterior processes.

There are few indications of muscle attachments on the pelvic girdle. Most of the iliac blade was presumably covered by the ilio-femoralis, as is typical for most non-mammalian therapsids (Romer 1922). Whether the pubo-ischio-femoralis internus attached to the ilium is unclear. The fossa on the medial surface of the pubis of NMQR 3189 has already been mentioned. It is near to the thickened anterior edge of the pubis, which is smoothly rounded. There



would be no barrier to a muscle that inserted on the medial surface of the pubis running over the anterior edge and inserting on the femur; this muscle was most probably the pubo-ischio-femoralis internus.

Kemp (1978) reconstructed the pubo-ischio-femoralis internus attaching on the lateral surface of the anterior process of the ilium in *Regisaurus*, whereas in the baurioid that he described (1986), which had much less-prominent anterior and posterior iliac processes, he considered that the pubo-ischio-femoralis internus attached to the medial side of the pubis. In the latter case, it is not clear what attached to the anterior iliac process. He considered that both of the animals in question had an essentially similar gait that could operate in both sprawling and parasagittal modes.

In order for the ventrally attaching pelvic muscles (pubo-ischio-femoralis internus and pubo-ischio-femoralis externus) to have adequate fibre-length when the femur is held in its parasagittal stance, the pubo-ischiadic plate must be oriented almost horizontally, and Kemp (1986) suggested that this was the case in the baurioid. It is impossible to demonstrate in NMQR 3189 how horizontally the pubo-ischiadic plate lay, although what reconstruction is possible suggests that it was not completely horizontal. There is, therefore, no compelling evidence that this particular animal had the parasagittal component of the dual-gait suggested by Kemp for the other therocephalians.

Both femora of NMQR 3189 are preserved but the proximal end is not well preserved on either bone. The femur (Fig. 10) is a slender bone with a gentle sigmoid curvature. What is preserved of the proximal end of the right femur indicates that there is a marked recess on the ventral surface, bounded posteriorly by the internal trochanter. It is difficult to assess how prominent the latter is since the bone is partially crushed. The trochanter major appears not to be well developed, although it is difficult to be sure of how complete it is. The head of the bone is not preserved. The distal end is expanded slightly and the distal condyles are weakly developed. The ventral surface of the distal end bears a shallow fossa. The shaft is approximately cylindrical in cross-section. The more complete right femur has a small portion missing from the shaft, so it is impossible to be certain of the exact orientation of the proximal and distal ends, but if the preserved position of the bone can be relied on, then the two ends were at a small angle to one another.

What is present of the femur resembles that of the baurioid described by Kemp (1986). Without a more complete proximal end, it is difficult to shed any further light on what kind of posture the hind limb adopted.

The tibia and fibula (Fig. 10) are both very slender, mediolaterally flattened bones. The smallest width of the tibia is approximately half that of the femur, that of the fibula approximately one-third that of the femur. The proximal end of the tibia is strongly expanded with a fairly prominent cnemial crest. The proximal end of the fibula is slightly expanded.

The pes is represented by the calcaneum and astragalus more or less *in situ* distal to the tibia and fibula (Fig. 10), and some separate metatarsals and phalanges that may not belong to the same foot. The calcaneum and astragalus are not well preserved and no details of their articular surfaces, nor a calcaneal heel, can be seen. Three (possibly four) metatarsals and three phalanges are present. The three metatarsals that can be definitely identified are relatively

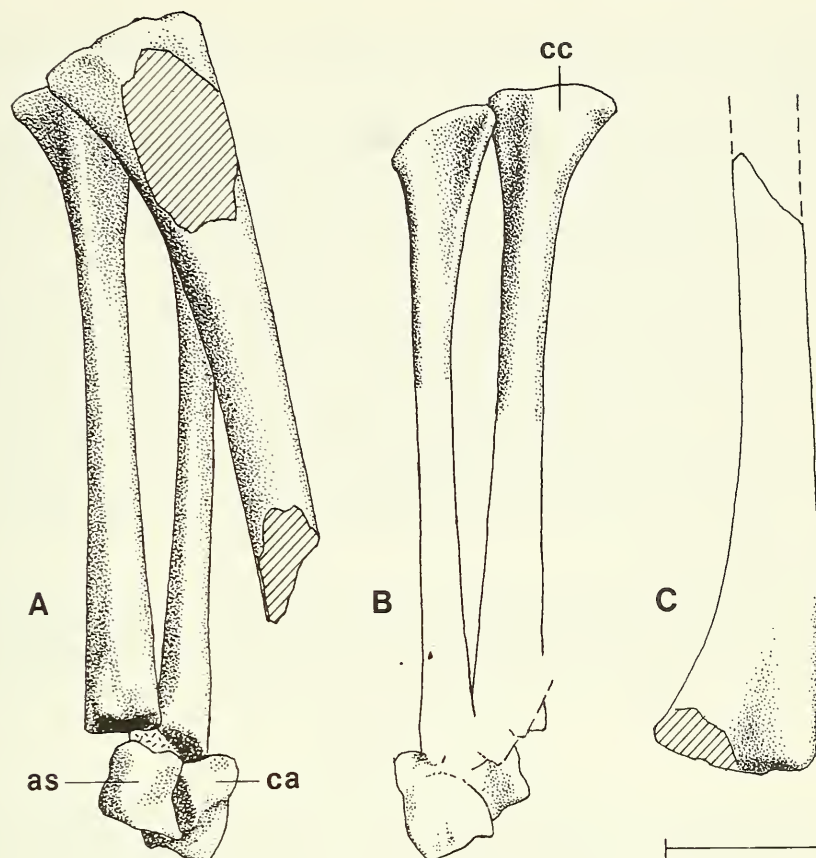


Fig. 10. The left femur, tibia and fibula of NMQR 3189. A. Distal part of femur in dorsal view, tibia and fibula in medial view. B. Tibia and fibula in lateral view. C. Distal part of femur in ventral view. Hatching indicates presence of matrix. Scale bar = 10 mm

long: approximately two-and-a-half times the length of the phalanges. The fourth possible metatarsal is much smaller and could therefore be either metatarsal I or II, or possibly a phalanx; the disarticulated state of the pes makes it impossible to tell which.

One ungual phalanx is present. It is bluntly pointed and approximately the same size as the unguis of the manus. What is preserved of the pes agrees broadly with that of *Bauria cynops* described by Broom (1937), Boonstra (1938) and Schaeffer (1941), although it is only two-thirds the length of that specimen.

### CONCLUSION

The postcranial skeleton of the late therocephalian described here shows some similarities with the earliest members of that group such as *Cynario-gnathus*. The latter form, from the *Tapinocephalus* zone (Cys 1967), is a larger animal than NMQR 3189, but the structure of the vertebral column and ribs is

essentially similar, including the abrupt transition in the posterior dorsal ribs. The scapula is also similar in bearing a depression on its lateral surface bounded by a ridge.

However, some differences between the two forms are also apparent. The humerus of *Cynariognathus* is a much more robust bone (although this might be expected in a larger animal) with more expanded ends and a shorter shaft region than in NMQR 3189 or the *Lystrosaurus*-zone regisaurid. The manus does not show the very small phalanges present in *Cynariognathus*, which appear to be a specialization of the *Tapinocephalus*-zone therocephalians.

The ilium of *Cynariognathus* is not well preserved, but Cys (1967) noted that it probably had little anterior extension. In the pristerognathid therocephalians described by Boonstra (1964), the anterior extension varies from being sharp and pronounced (*Cynariognathus*, unidentified pristerognathid) to undeveloped (*Pristerognathoides*). This feature cannot be verified in NMQR 3189, but in *Regisaurus* and the regisaurid described by Kemp, there is a pronounced anterior extension of the ilium. The obturator fenestra is thought to be a small perforation in *Cynariognathus*, whereas in NMQR 3189 (if the pubis has been identified correctly) the fenestra is large. It is also large in the regisaurid specimen.

Some of these features (e.g. the presence or absence of an anterior extension of the ilium) are obviously concerned with the changing of muscle attachments, but what this means in terms of evolution of locomotory ability within the group must await an in-depth functional study of therocephalian postcrania.

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### ABBREVIATIONS

as	—	astragalus	is	—	ischium
ca	—	calcaneum	j	—	lower jaw (dentary)
cc	—	cnemial crest	ma	—	manus
cl	—	clavicle	mt	—	metatarsals
dep	—	depression on scapula	pt	—	proximal tarsals
dpc	—	delto-pectoral crest of humerus	ra	—	radius
ent.f	—	entepicondylar foramen of humerus	ri	—	scapular ridge
fe	—	femur	sc	—	scapula
fi	—	fibula	t	—	tooth
fs	—	flat surface of scapula	ti	—	tibia
hd	—	head of humerus	ul	—	ulna
hu	—	humerus	v	—	vertebra
il	—	ilium	ve	—	vertebrae